Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus)

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Abstract

We examined the patterns of habitat-specific mortality for newly settled red drum (*Sciaenops ocellatus*) using an experimental mesocosm approach. Experiments were designed to analyze prey vulnerability and fish rearing-type (wild-caught or hatchery-reared) in estuarine habitats of varying structural complexity including marsh (*Spartina alterniflora* Loisel), oyster reef (*Crassostrea virginica* Gmelin), seagrass (*Halodule wrightii* Aschers), and nonvegetated sand bottom. We used two different predators, pinfish (*Lagodon rhomboides* Linnaeus) and spotted seatrout (*Cynoscion nebulosus* Cuvier). For both predators, vulnerability of wild-caught red drum was significantly lower in structurally complex habitats such as seagrass and oyster reef; the highest vulnerability was associated with the nonvegetated bottom. This habitat effect was not apparent for hatchery-reared prey. In trials using a combination of both rearing-types, there was no significant habitat effect on prey selection, but hatchery-reared red drum suffered higher overall mortality than wild-caught fish from pinfish predators. In these trials, spotted seatrout did not select for either prey type. Differences we observed in prey vulnerability were likely caused by behavioral differences between wild-caught and hatchery-reared red drum. Our results reinforce the conclusion that structural complexity in estuarine habitats increases survival of newly settled fishes. Our data also suggest that hatchery-reared red drum may be more vulnerable to predation than natural fishes, and that survival of stocked fish may be enhanced through habitat-related behavior modification. Published by Elsevier Science B.V.

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1. Introduction

Predation can be a major factor contributing to variability in survival of newly settled marine organisms (Cushing, 1975; Houde, 1987) and can affect the recruitment and abundance of marine fishes (Bailey and Houde, 1989; Leggett and Deblois, 1994). The ability of juvenile fish to avoid predators is often related to the complexity of available habitat structure (Crowder and Cooper, 1982; Salvino and Stein, 1982; Nelson and Bonsdorff, 1990; Heck et al., 1997). Structural complexity can affect the foraging efficiency, effectiveness, and selectivity of predators (Heck and Thoman, 1981; Crowder and Cooper, 1982; Orth et al., 1984; Werner and Gilliam, 1984; Eggleston et al., 1998). Highly structured habitats may also support increased growth (Heck and Thoman, 1981; Rozas and Odum, 1988; Levin, 1994), and rapid growth may reduce mortality by size-selective predators (Werner et al., 1983; Holbrook and Schmitt, 1988; Levin et al., 1997; Sogard, 1997). For a variety of reasons, therefore, mortality rates of young fishes should be relatively low in highly structured habitats (Shulman, 1984; Bell and Westoby, 1986; Hixon and Beets, 1989; Connell and Jones, 1991; Eggleston, 1995; Heck et al., 1997).

The red drum, *Sciaenops ocellatus*, is an estuarine-dependent sciaenid common to the Gulf of Mexico and southeastern U.S., and this species supports an important recreational fishery (Pattillo et al., 1997). Red drum spawn during early fall in coastal waters near passes and inlets (Peters and McMichael, 1987; Comyns et al., 1991). Currents carry eggs and pelagic larvae into bays and estuaries, where they settle (ca. 6–8 mm) primarily into seagrass meadows when available (Holt et al., 1983; Rooker and Holt, 1997).

In the Galveston Bay system of Texas, seagrass cover has declined approximately 80% during the past three decades leaving seagrass meadows restricted to small areas in Christmas Bay (Adair et al., 1994; Sheridan et al., 1998). Despite this paucity of seagrass, the system continues to support large populations of red drum (Fuls and Hensley, 1998), suggesting that new settlers are using alternative nursery habitats. Galveston Bay has large expanses of salt marsh, oyster reef, and nonvegetated bottom, and understanding predation rates associated with these alternative habitats is important in determining their role as potential nursery areas for red drum.

Over the past two decades, fisheries managers in Texas have attempted to increase red drum recruitment and stock size by releasing hatchery-reared juveniles in estuaries to artificially enhance natural stocks (McEachron et al., 1998). Stock enhancement can be a valuable tool in the management of marine fisheries (Secor and Houde, 1998; Travis et al., 1998), but the benefits of stock enhancement for red drum have been questioned (Grimes, 1998). One question that should be addressed is whether survival of hatchery-reared red drum is similar to that of natural fish (McEachron et al., 1998). Behavioral mechanisms for reducing predation may be compromised by the hatchery experience (Munro and Bell, 1997); and evidence from salmonids suggests that predation on hatchery-reared fish is relatively high, because these fish have a reduced ability to recognize and avoid predators (Olla et al., 1998).

Measuring predation in natural systems is often difficult (Houde, 1987), however, laboratory mesocosm studies have been successfully used to assess prey vulnerability in

relation to different habitat types (Cowan et al., 1992; Carr and Hixon, 1995; Elliot and Leggett, 1996; Rooker et al., 1998). Our goal was to experimentally examine predation-related mortality of young red drum within different estuarine habitat types using laboratory mesocosms. Specifically we tested whether (1) predation-related mortality differs among seagrass, oyster reef, salt marsh, and nonvegetated bottom; and (2) the protective value of habitat types is different for wild-caught and hatchery-reared red drum.

2. Methods

2.1. Experimental organisms

We obtained hatchery-reared red drum from the Texas Parks and Wildlife Seacenter Texas hatchery in Lake Jackson, TX. These fish were reared from captive induced spawns, where eggs were collected and hatched in 380-l tanks. After 36 h, larvae were then transferred to 0.4-ha polyethylene-lined ponds and fed wild zooplankton and commercial fry feed (Rangen). We collected red drum from these ponds with dip nets when fish were about 20–30 days old (15–25 mm SL). We seined wild red drum (of a similar size) and fish predators from salt marsh and seagrass meadows in Galveston Bay, TX. We selected pinfish, *Lagodon rhomboides*, (ca. 80–100 mm SL) as the primary predator in this study, because this species is an abundant natural predator of young red drum (Fuiman, 1994; Rooker et al., 1998). Another predator on young red drum, the spotted seatrout *Cynoscion nebulosus* (ca. 80–120 mm SL), was also used in one experiment. Prior to use in experiments, we held all fish for 1–7 days in flow-through fiberglass tanks located in a large wet-lab facility. The sand-filtered seawater (25–30‰; 24–28°C) used in the facility was pumped from the Gulf of Mexico. We fed fish daily with frozen or live food; red drum were fed mysid shrimp, and predators were fed grass shrimp (*Palaemonetes* spp). Fish were used only once in an experiment, and with the exception of hatchery-reared red drum, survivors were released into Galveston Bay.

2.2. Experimental mesocosms

We constructed 20 experimental mesocosms in 125-l cylindrical plastic tanks (60-cm diameter × 44 cm deep). To minimize the complication of alternative foods on predation rates, we attempted to simulate only the structure of each of the four habitat types. The nonvegetated habitat type was constructed by adding 10 cm of washed beach sand, and other habitats were constructed on a foundation of this sand. We simulated oyster reef by scattering a 5-l bucket of oyster shells (sun dried and washed) over the bottom of a mesocosm using the excess shells to build an elevated reef-like structure. We simulated salt marsh by planting cut *Spartina alterniflora* culms (sun dried for at least 14 days) into sand at a mean density of 474 stems m^{-2} (134 per mesocosm); this density corresponded to natural densities in a Galveston Bay salt marsh. Seagrass cores (*Halodule wrightii*) were collected from Galveston Bay, washed free of animals and detritus, and transplanted into mesocosms at a mean shoot density of 9945 m^{-2}

(SE = 334). Each habitat type was randomly assigned and constructed in five replicate mesocosms. The mesocosms were filled with approximately 30 cm of filtered seawater (25–30‰ and 24–28°C). Light was supplied by skylights and florescent bulbs with levels ranging from 10–12 $\mu E\ s^{-1}\ m^{-2}$.

2.3. Control trials

Predation rates were determined by counting the remaining prey in each mesocosm following an experiment, and we assumed 100% recovery efficiency. We measured our recovery efficiency in control trials without predators using one mesocosm of each habitat type during the mixed trial experiment and with 10 hatchery-reared fish. There was no evidence of non-predatory mortality, and we recovered all 40 prey fish. Therefore, control mesocosms were not included with subsequent experimental trials.

2.4. Predation trials

Ten red drum were placed in each mesocosm (35 prey m^{-2}). These red drum densities were higher than reported for wild populations (Minello, 1999; Stunz, 1999); but densities approaching this magnitude have been reported for other sciaenid juveniles in estuarine habitats (Rooker et al., 1998). After a 2-h acclimation period, we introduced two predators into each mesocosm. We allowed the predators and prey to interact for 6 h, removed predators using a dip net, and drained the mesocosms to collect the remaining prey. We then repeated the entire experimental trial on a second day. In each experiment (two trials), therefore, we had 10 replicate observations per habitat type. We also ran control trials without predators to examine mortality unrelated to predation and evaluate recovery efficiency in different habitat types.

We ran separate experiments to examine habitat-specific mortality rates on both wild-caught and hatchery-reared red drum using pinfish predators. To more directly evaluate the relative vulnerability of rearing-type, we also ran an additional experiment with pinfish predators using both prey types simultaneously (five hatchery-reared and five wild-caught red drum). In this experiment, prey fish were marked using an anal fin clip to distinguish rearing-type. An experiment using both prey types simultaneously was also conducted with spotted seatrout as the predator.

2.5. Statistical analyses

We used analysis of variance (ANOVA) to test the hypothesis that red drum mortality did not vary among habitat types; the number of fish eaten per trial was the response variable. In trials where both prey rearing-types were present simultaneously, we also analyzed the percent of wild-caught fish eaten in a mesocosm to examine the effect of habitat type on prey selection by predators. We used Hartley's F-max to test for homogeneity of variances (Milliken and Johnson, 1984) and failed to reject the null hypotheses of equality ($P > 0.17$). Thus, we did not transform the data in these analyses. We examined significant ($P < 0.05$) habitat effects with Fisher's protected least significant difference (PLSD) to test for differences among treatment means. A

significance level of 0.01 was used in these PLSDs to buffer against problems caused by multiple testing and uncontrolled experimentwise error (Day and Quinn, 1989). We used
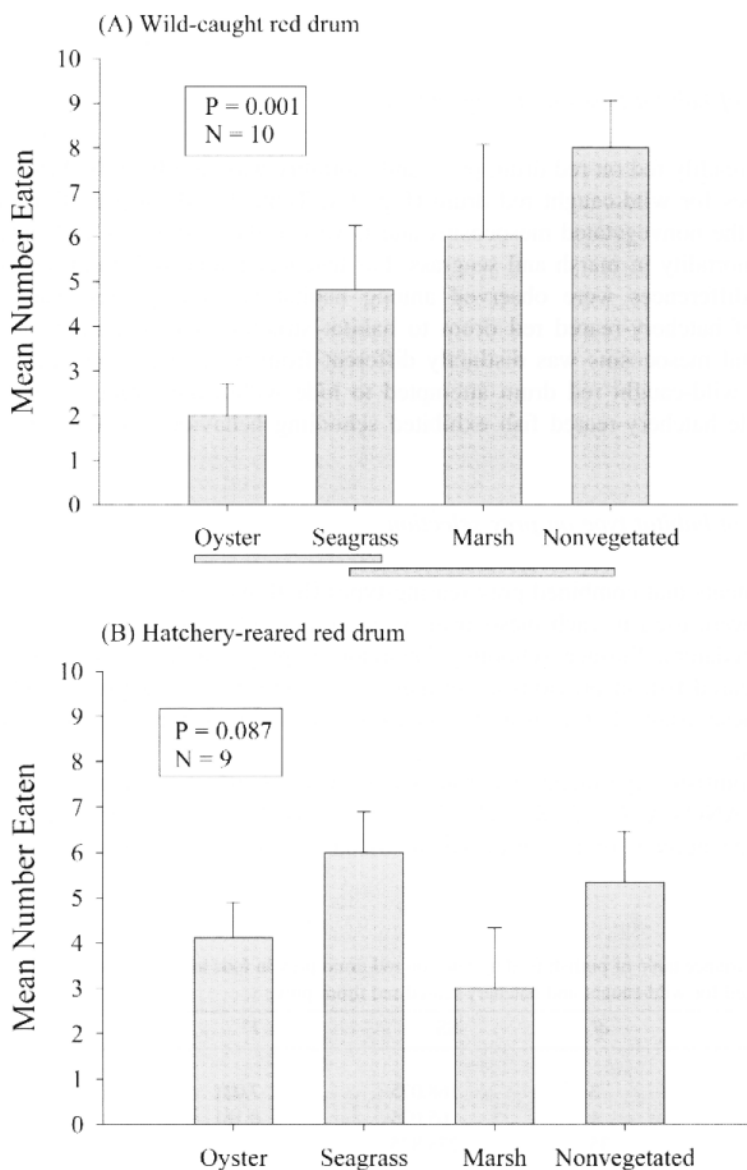

Fig. 1. Feeding rates of pinfish on red drum prey in four habitat types (mean number of prey eaten ± SE). Separate experiments were conducted for wild-caught (A) and hatchery-reared (B) prey. The number of replicate mesocosms for each treatment is indicated by N. The P-value is from an ANOVA comparing mean number eaten among all four habitats. Horizontal lines below the bars are the results of Fisher's PLSD, and bars sharing the same lines are not significantly different (P > 0.01).

paired Student's *t*-tests to examine the relative vulnerability of red drum rearing-type to predators, irrespective of habitat type.

3. Results

3.1. Effect of habitat type on prey mortality

Pinfish readily fed on red drum prey, and mortality was significantly different among habitat types for wild-caught red drum (Fig. 1A, Table 1). Mean predation rates were highest in the nonvegetated mesocosms and lowest in the oyster reef with intermediate levels of mortality in marsh and seagrass. For hatchery-reared red drum, no significant mortality differences were observed among habitat types (Fig. 1B, Table 1). The response of hatchery-reared red drum to habitat structure and to pinfish predators in experimental mesocosms was distinctly different from wild-caught red drum. Without exception, wild-caught red drum attempted to hide within the structure of the habitat types, while hatchery-reared fish exhibited schooling behavior near the surface of the water.

3.2. Effect of habitat type on prey selection

Experiments that combined prey rearing-types (both hatchery-reared and wild-caught red drum were used in each mesocosm) were conducted with both pinfish and spotted seatrout predators. Surface schooling behavior of prey (similar to that displayed by hatchery-reared fish in previous experiments) was observed for approximately half the prey in these trials, but it was not possible to distinguish rearing-type during the experiment.

In the pinfish experiment, we found a significant effect of habitat type on prey mortality (ANOVA $F = 2.884$, $df = 3,35$, $P = 0.049$) if we ignored rearing-type and analyzed the number of red drum eaten. Mean mortality rates were lowest in oyster

Table 1
Analysis of variance table of pinfish feeding rates on red drum prey in four habitat types. Separate experiments were conducted for wild-caught and hatchery-reared red drum prey

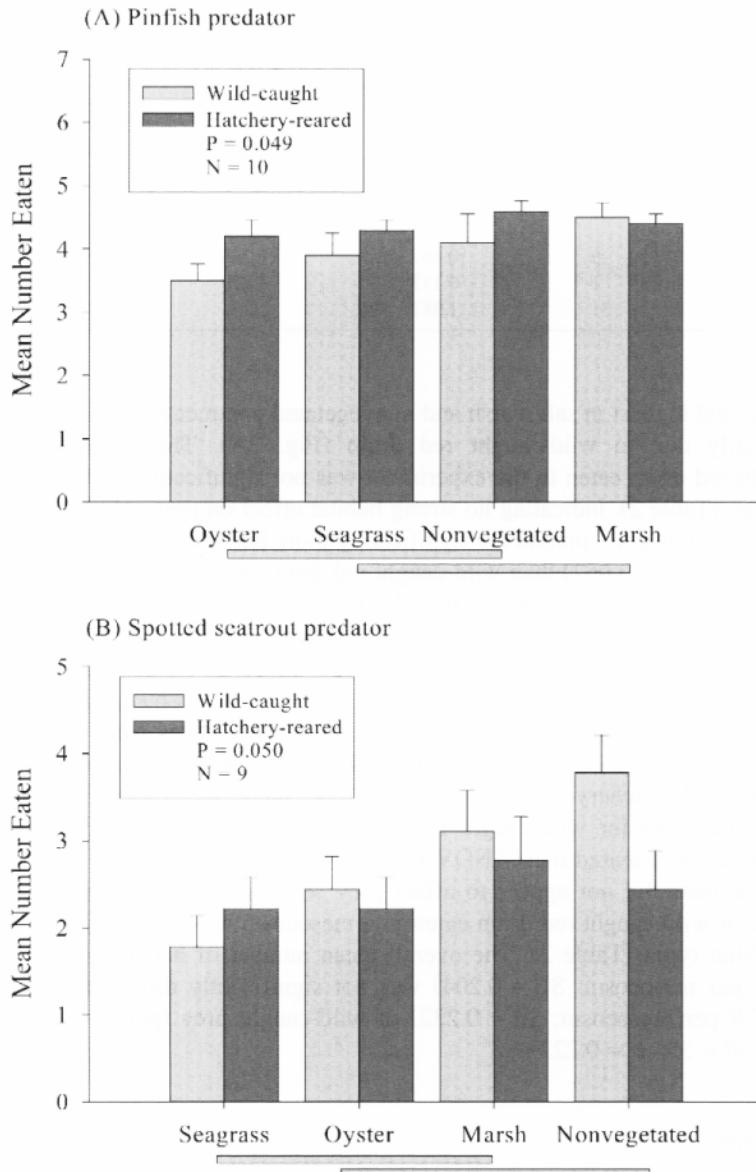| Source	df	SS	F	P
Wild-caught:				
Habitat type	3	168.075	7.031	0.001
Day (block)	1	65.025	8.161	0.007
Residual error	35	278.875		
Hatchery-reared:				
Habitat type	3	58.083	2.400	0.087
Day (block)	1	72.835	9.030	0.005
Residual error	31	250.054		

Fig. 2. Feeding rates of pinfish and spotted seatrout predators on mixed red drum prey (five wild-caught and five hatchery-reared) among four habitat types (mean number of prey eaten ± SE). Separate experiments were conducted for pinfish and spotted seatrout predators. The number of replicate mesocosms for each treatment is indicated by N. The P-value is from an ANOVA comparing overall mean number eaten among all four habitats. Horizontal lines below the bars are the results of Fisher's PLSD, and bars sharing the same lines are not significantly different ($P > 0.01$).

Table 2
Analysis of variance table of observed feeding rates on percent wild-caught red drum prey by pinfish and spotted seatrout predators among the various habitat types during mixed rearing-type experiments (five wild-caught and five hatchery-reared red drum). Separate experiments were conducted for pinfish and spotted seatrout predators

Source	df	SS	F	P
Pinfish:				
Habitat type	3	0.011	0.902	0.450
Day (block)	1	0.055	13.967	0.001
Residual error	35	0.137		
Spotted seatrout:				
Habitat type	3	0.167	1.248	0.309
Day (block)	1	0.173	3.879	0.058
Residual error	31	1.381		

mesocosms and highest in salt marsh and nonvegetated treatments, and this habitat effect was primarily due to wild-caught red drum (Fig. 2A). The mean percentage of wild-caught red drum eaten in the experiment was not significantly different among the habitat types (Table 2), indicating no strong habitat effect on prey selection. Irrespective of habitat type, however, pinfish ate significantly more hatchery-reared fish (mean of 4.8 per mesocosm; $SE = 0.067$) than wild-caught red drum (4.0 per mesocosm; $SE = 0.072$) (paired Student's t-test, $t = -4.78$, $df = 39$, $P < 0.001$).

The number of red drum eaten by spotted seatrout was also significantly different among habitat types (ANOVA $F = 2.898$, $df = 3,31$, $P = 0.050$; Fig. 2B). Mean predation rates were lowest in seagrass and oyster mesocosms and highest in the nonvegetated and salt marsh treatments; again, these differences were primarily due to the presence of the wild-caught red drum (Fig. 2B). If we analyzed mortality for wild-caught and hatchery-reared prey separately, there were significant differences among habitat types for wild-caught fish (ANOVA $F = 4.922$, $df = 3,31$, $P = 0.006$) but not for hatchery-reared fish (ANOVA $F = 0.403$, $df = 3,31$, $P = 0.752$; Fig. 2). The habitat treatments did not appear to affect prey selection by spotted seatrout, and the percentage of wild-caught red drum eaten in a mesocosm was not significantly different among habitat types (Table 2). The overall mean number of hatchery-reared red drum eaten (2.4 per mesocosm; $SE = 0.204$) was not significantly different from the mean number (2.8 per mesocosm; $SE = 0.232$) of wild-caught prey (paired Student's t-test, $t = 1.243$, $df = 35$, $P = 0.222$).

4. Discussion

Our study provides additional evidence that habitat structure is an important requirement for reducing mortality of newly settled wild red drum. Lower mortality rates for wild-caught red drum were observed in structured habitat types compared with nonvegetated mesocosms using both pinfish and spotted seatrout predators. Structural complexity of habitats has been shown to reduce predation rates on a variety of aquatic prey (Heck

and Thoman, 1981; Crowder and Cooper, 1982; Minello and Zimmerman, 1983; Salvino and Stein, 1982; Nelson and Bonsdorff, 1990; Barshaw et al., 1994; Beck, 1995; Heck et al., 1997). Field tethering experiments with mummichogs *Fundulus heteroclitus* (Rozas and Odum, 1988), brachyuran and anomuran crabs (Heck and Thoman, 1981), and penaeid shrimp (Minello, 1993) have documented significantly lower predation rates in submerged aquatic vegetation and emergent marsh than on nonvegetated bottom. In laboratory experiments with newly settled red drum, Rooker et al. (1998) also found lower mortality rates in seagrass versus nonvegetated treatments using pinfish predators. Mortality of wild-caught red drum in our experiments was lowest in seagrass and oyster treatments. For visual predators, such as pinfish and spotted seatrout (Chao and Musick, 1977), these habitat types probably provide prey with more protection than the less complex salt marsh and nonvegetated bottom.

Reduced mortality in structured habitat types should result in increased densities. In estuaries of Texas and Louisiana, juvenile red drum are generally most abundant in seagrass beds (Rooker and Holt, 1997; Minello, 1999). However, Baltz et al. (1993) and Stunz (1999) also found high densities near the marsh edge ecotone. When seagrass coverage is limited, alternative structurally complex habitat types, such as salt marsh and oyster reef, may function as nurseries for red drum.

Our study specifically addressed the relative mortality and vulnerability of wild-caught and hatchery-reared red drum. Rearing-type appeared to alter the habitat effect on mortality rates. Wild-caught red drum had lower mortalities in the structurally complex habitat types. In contrast, hatchery-reared red drum were equally vulnerable in the four estuarine habitat types to both pinfish and spotted seatrout predators. In mixed trial experiments, we found no significant habitat effects on prey selection by pinfish or spotted seatrout. For pinfish, however, the overall vulnerability of hatchery-reared red drum was greater than wild-caught fish.

Mortality differences between rearing-types may be related to behavioral responses of the red drum to the presence of habitat structure. When wild-caught red drum were introduced into the mesocosms, they exhibited a cryptic behavioral response by immediately swimming to the bottom and remaining there. In contrast, hatchery-reared fish schooled at the surface, and predators had access to these prey regardless of the habitat type. This surface schooling behavior especially may have increased vulnerability of hatchery-reared fish to aggressive pinfish predators that commonly feed in the water column. Spotted seatrout were less aggressive, remained in close proximity to the substrate, and appeared more reluctant to move up into the water column after hatchery-reared prey. This reluctance of spotted seatrout to leave the substrate in our mesocosms may explain why, although there was no significant prey selection, seatrout ate more wild-caught than hatchery-reared prey.

Development of predator avoidance behavior in fishes appears to be linked to early life experiences (Huntingford and Wright, 1993; Fuiman and Magurran, 1994). Based on a settling length of 8 mm (SL) and a growth rate of ~ 0.5 mm/day (Rooker and Holt, 1997; Stunz, 1999), the wild-caught red drum used in our experiments had settled into structured benthic habitats of Galveston Bay at least 2 weeks before they were collected. The hatchery-reared fish, however, came from ponds with little habitat structure and few predators, and these fish may have been deprived of necessary stimuli needed to develop

predator avoidance tactics (Munro and Bell, 1997; Olla et al., 1998). Patten (1977) and Suboski and Templeton (1989) found that hatchery-reared coho salmon *Oncorhynchus kisutch* were more vulnerable to predation than wild-caught fish. Rooker et al. (1998) suggested hatchery-reared red drum were more vulnerable to predators than wild-caught fish, and our results support this conclusion.

Mesocosms are useful for examining mortality in structurally complex habitats, but extrapolation of results to field conditions can be risky. In addition to the experimental artifacts inherent in enclosure studies (Peterson and Black, 1994), we did not examine environmental or additional trophic interactions, which can also contribute to natural predation-related mortality. For example, water depth (Ruiz et al., 1993) and turbidity (Gregory and Northcote, 1993; Benfield and Minello, 1996) can influence predation rates and may vary with habitat structure in estuaries. Food availability varies among estuarine habitat types, and abundant alternative prey may reduce predation pressure on other prey species. In addition, prey using structurally complex habitats such as marsh and submerged aquatic vegetation may have increased growth rates (Boesch and Turner, 1984; Orth et al., 1984; Rozas and Odum, 1988; Levin et al., 1997). Stunz (1999) found higher growth rates for red drum in seagrass and marsh habitats, and increased growth may result in lower mortality by reducing the amount of time spent in smaller and more vulnerable size classes.

Our results suggest that both structural complexity of available habitats and early life history experiences of red drum can affect predation-related mortality. Young red drum collected after settlement in natural habitats exhibit cryptic behavioral responses and apparently use habitat structure to reduce predation. In contrast, hatchery-reared red drum behave differently in relation to simulated laboratory habitats, and do not appear to derive the same protective benefits from habitat structure. These differences suggest that stock enhancement programs for this species may benefit from modifications designed to alter behavioral responses of hatchery-reared red drum to habitat structure. Our results also indicate that oyster reefs, and to a lesser extent salt marshes, can function like seagrass beds to provide protective habitat structure for juvenile red drum. In estuaries without extensive seagrass beds, such as Galveston Bay, these alternative habitat types may provide important nursery functions for this species.

Acknowledgements

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